

**FINAL REPORT**  
**BARD PROJECT US-2659-95**  
**October 1, 1996 - January 31, 2000**

**Sub-specific populations of *Verticillium dahliae* and their  
roles in vascular wilt pathosystems**

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**Abstract**

*Verticillium dahliae* is an economically important pathogen causing vascular wilt on over 160 plant species. In North America, potato early dying is a significant disease of potato, especially in the midwest and Pacific northwest states. This disease is caused by the fungus *Verticillium dahliae* and in some cases involves a synergistic interaction with root-lesion nematodes, primarily *Pratylenchus penetrans*. In Israel, *Verticillium* wilt occurs in many regions and inflicts serious losses in potato, cotton, and other crops. Objectives of this project were to establish a large collection of isolates of *Verticillium dahliae* from potato (USA) and several host plants (Israel) and to characterize and compare the isolates with regard to morphology, vegetative compatibility group (VCG), and pathogenic capabilities on several hosts. Isolations were made from 224 commercial lots of certified potato seed tubers from across N. America and 87 potato fields located in the Columbia Basin of Oregon and Washington. A large collection of isolates from central U.S. states already existed. In Israel, 47 field sites were sampled and isolates of *Verticillium dahliae* were recovered from 13 host plant species and from soil. Potato isolates from N. America were tested for vegetative compatibility and all found to be in VCG 4 with about 2/3 in VCG 4A and the rest in VCG 4B. VCG 4A isolates were significantly more aggressive on potato than VCG 4B isolates and were more likely to interact synergistically with *P. penetrans*. The Israeli isolates fell into three vegetative compatibility groups. Nearly all (> 90%) VCG2B and VCG 4B isolates were recovered from the northern and southern parts of Israel, respectively, with some overlap in central areas. Several pathotypes were defined in cotton, using cotton and eggplant together as differentials. All VCG 2B isolates from cotton caused severe disease in cotton, while VCG 2A and VCG 4B isolates from several crops were much less aggressive to cotton. When Israeli isolates of VCGs 2A, 2B and 4B were inoculated to potato and tomato, VCG 4B isolates caused much more severe disease on potato and VCG 2A isolates caused much more severe disease in tomato. Differential patterns of pathogenicity and aggressiveness of these VCGs on potato and tomato were consistent regardless of the host plant of origin. Isolates of the same VCG resembled one another more than isolates from different VCGs based on colony and microsclerotial morphology, temperature responses and, partially, in pathogenicity. Vegetative compatibility grouping of *V. dahliae* in Israel appears closely associated with specific pathogenicity and other phenotypic traits. The absence of VCG 4A in Israel is significant. VCG patterns among *Verticillium* populations are useful to predict relatedness and pathogenic potential in both countries.

**Achievements**

*Verticillium dahliae* is an economically important pathogen causing vascular wilt on over 160 plant species. In North America, potato early dying is a significant disease of potato, especially in the midwest and Pacific northwest states. This disease is caused by the fungus *Verticillium dahliae* and in some cases involves a synergistic interaction with root-lesion nematodes, primarily *Pratylenchus penetrans*. In Israel, *Verticillium* wilt occurs in many regions and inflicts serious losses in potato, cotton, avocado, olives and some vegetable and flower crops. Substantial losses (20-40% yield reduction) are quite common in areas with frequent cropping of susceptible crops. Effective and economic management strategies for *Verticillium* wilt are not available in some crops and in some involve the use of highly toxic fumigants such as metham sodium or methyl bromide. The latter is suspected of depleting the ozone layer and is planned for phase-out by 2005. Tomato, so far the only crop in which race-specific resistant cultivars are available, is threatened by spread of the highly virulent race 2. A thorough understanding of the biology and genetic variability of *V. dahliae* can assist in developing improved disease management tools including resistant cultivars and preventing pathogen dissemination. We studied the distribution of *V. dahliae* populations in potato production areas in N. America and across several crop-production areas in Israel. Phenotypes of isolates were characterized and relatedness among genetic populations were determined and compared with respective known genetic groups of the pathogen by using international testers developed by the P.I. (R. Rowe) and coworkers in Ohio. This is the first comprehensive study of *V. dahliae* populations in Israel, and similar to a previous study done by T. Katan and coworkers on *Fusarium* (partially funded by BARD).

In addition to the scientific value of our findings, the knowledge gained may lead to several potential applications. In the short term, the detection of isolates highly virulent to cotton in the northern part of Israel stimulated the authorities and the cotton-growers' association to take measures to avoid spread of these strains to other areas. A greater emphasis now being placed on sanitation practices should have implications on other pathogens as well. Farmers are now more careful in choosing their plots to avoid infested soils. Developing resistant cotton cultivars is a long-term project, and breeders are now aware of the diversity that exists among populations of this pathogen, which must be considered while searching for more tolerant cotton cultivars. Furthermore, our findings on the geographic distribution of important strains of *V. dahliae* are

essential for developing decision-making tools, e.g. allocation of soils for different crops, and application of expensive control measures.

With regard to potatoes, several of our findings have important applications in disease management. Implications for the North American potato industry are considerable. Extensive infection of seed potatoes with *V. dahliae* certainly explains the widespread distribution of VCG 4A strains across U.S. and Canadian potato production regions. It also brings into question the importance of seedborne as compared with soilborne inoculum of *V. dahliae*, the latter being the target of most current control practices. Considerable resources are expended annually in some production regions to apply soil fumigants to fields prior to planting potatoes for control of potato early dying. The importance of seedborne inoculum in the development of potato early dying following fumigation warrants investigation. The use of disease-resistant cultivars is the most practical disease management strategy and efforts are ongoing to develop cultivars with improved resistance to *Verticillium* and high market acceptance. Better understanding of the genetic diversity that exists among populations of *V. dahliae* that cause potato early dying and the use by breeders of the most aggressive strains, ie. VCG 4A, in screening germplasm will be essential to accomplish this goal. It is particularly noteworthy that VCG 4A strains were not found in Israel and potatoes were found to be infected only with VCG 4B. This probably reflects the rare movement of seed tubers from N. America to Israel where reliance is primarily on seed grown locally or in Europe. Vigilance on the part of pathologists in Israel is needed to prevent the introduction of this particularly aggressive strain.

Cooperation among scientists took place throughout the project duration, including periodic meetings at international conferences. Exchange of cultures, information and advice between the partners occurred on many occasions.

## **Background, scientific and agricultural relevance of the project.**

*Verticillium dahliae* is an economically important pathogen causing vascular wilt on more than 160 plant species (21). In North America, potato early dying is a significant disease of potato, especially in the midwest and Pacific northwest (17,18). Potato early dying is caused by the fungus *Verticillium dahliae* and in some cases involves a synergistic interaction with root-lesion nematodes, primarily *Pratylenchus penetrans*. In recent years, research in several laboratories has demonstrated the existence of considerable pathogenic variability among strains of *V. dahliae*. Ohio studies, using vegetative compatibility analysis, have shown that isolates of *V. dahliae* from Ohio and other midwestern states from soil and several crops fall into several vegetative compatibility groups (VCGs). However, only those in VCG 4 are significant in causing disease on potato -- primarily those in VCGs 4A and 4B. Pathogenicity tests with these isolates showed that all were pathogenic to potato, but those in VCG 4A were collectively more aggressive and likely composed a host-adapted pathotype (9,10). These findings have been confirmed by subsequent studies in other states (22,23). Ohio studies have also shown that the synergistic interaction between *V. dahliae* and *P. penetrans* appears to be restricted to, or at least much more severe with, *V. dahliae* isolates of VCG 4A (3). Just recently, Ohio and Ontario, Canada, research has demonstrated that these two strains can be reliably identified by molecular markers (7). In Israel, *Verticillium* wilt occurs in many regions and inflicts serious losses in potato, cotton, and some other crops (2, 12, 15, 24).

In view of its broad host range and apparently low host specificity, *V. dahliae* had been considered to have little genetic diversity within populations. However, more recent vegetative-compatibility and molecular studies suggest that significant genetic diversity does exist in *V. dahliae* (11, 19). Vegetative compatibility refers to the ability of individual fungal strains to undergo mutual hyphal anastomosis, which results in viable heterokaryons (11). When a heterokaryon is established, the participating isolates are placed in the same vegetative compatibility group (VCG). In *V. dahliae*, an anamorphic fungus with no known sexual stage, hyphal anastomosis and heterokaryosis are the only means of exchanging genetic information among different strains. Thus, strains belonging to the same VCG have the potential to share a common gene pool separated from the gene pools of other VCGs. Using nitrate-nonutilizing (*nit*) mutants, three to five VCGs have been identified among *V. dahliae* strains from diverse

geographic and plant sources worldwide (9, 10, 11, 19). A set of isolates and *nit* mutant testers that represents all known VCGs was described by Rowe and coworkers (9, 10).

The objectives of this study were to assemble a large, diverse collection of *V. dahliae* strains from potatoes in N. America and from several host plants in Israel and then (i) determine the diversity of VCGs in *V. dahliae* in both countries and their relatedness to internationally recognized VCGs; and (ii) reveal any association between VCG, host-plant origin, regional distribution, growth characteristics, virulence in this population, and the ability of representative isolates to interact with the root-lesion nematode *Pratylenchus penetrans*.

### **Methodologies and materials.**

Samples were collected from 224 commercial lots of certified potato seed tubers obtained from western North American seed production areas (nine U.S. states and two Canadian provinces) and from eastern seed production areas (eight U.S. states and two Canadian provinces). Twenty-tuber samples were selected randomly from each seed lot and surface disinfested. Vascular tissues were excised aseptically from beneath the stem end of each tuber for pathogen isolation. Soil samples collected from 87 potato fields located across the Columbia Basin of Oregon and Washington were assayed on a semi-selective medium. Selected colonies of *V. dahliae* were removed and purified to develop a representative collection of several hundred isolates. In Israel, plant samples were collected from crops growing in various regions across the country. Isolations were made from potato, cotton, eggplant, tomato, peanut, pepper, chrysanthemum, watermelon and various weeds and soil. Methods of isolation of *V. dahliae* from plants and soil, generation and characterization of *nit* mutants, vegetative compatibility grouping, pathogenicity tests and field microplot techniques were as described elsewhere (2, 3, 4, 9, 12, 13, 14, 25). The development of an improved medium for selecting nitrate-nonutilizing (*nit*) mutants of *V. dahliae*, which was developed in the framework of this project (13), was used in the Israeli studies.

### **Results**

*V. dahliae* was isolated from 65 of the 224 potato certified seed lots grown in commercial production areas across North America - - a successful isolation rate of nearly 30% (16, 20) When grown on chlorate-amended medium, mycelial growth of all isolates was restricted due to chlorate

sensitivity and mutant cells unable to metabolize chlorate emerged as fast-growing sectors from the edges of the restricted wild-type colonies. At least one *nit* mutant was recovered from each isolate. Approximately five times more *nit1* mutants than *nitM* mutants, and only a few *nit3* mutants, were recovered. No isolate yielded more than one *nit* mutant phenotype. Recovered *nit* mutants were paired with standard tester strains to determine the VCG of each isolate based on complementation. All 162 *V. dahliae* isolates tested were VCG 4 with nearly two thirds belonging to VCG 4A (16, 20). In two cases (British Columbia and Oregon) both VCG 4A and 4B isolates were recovered from the same seedlot. Microsclerotial abundance and shape, as well as colony appearance and morphology of wild-type growth of each isolate were evaluated. There appeared to be no obvious correlation between VCG classification and the morphology and growth pattern of the *V. dahliae* isolates tested. Although isolates were obtained from a wide range of potato cultivars grown across North America, there was no correlation between VCG and cultivar or location. Soil samples from the Columbia Basin yielded populations of *V. dahliae* that ranged from 0 to 169 cfu/g of soil (mean 14 cfu/g). Over 200 isolates of *V. dahliae* were recovered from soil. *Nit* mutants recovered from each were paired with standard testers and all belonged to VCG 4 with two thirds in VCG 4A.

In Israel, a total of 565 isolates of *V. dahliae* from 47 locations across the country were recovered from potato (42%), cotton (33%), eggplant, tomato, peanut, pepper, chrysanthemum, watermelon, weeds and soil (12). Water-agar-chlorate (WAC) medium was developed in this project for generating *nit* mutants from *V. dahliae* (13), and at least one *nit* mutant was recovered from each of the 565 *V. dahliae* isolates. Complementary *nit* mutants (*nit1* and *NitM*) derived from each isolate were paired in various inter-isolate combinations. Based on positive complementation reactions, three VCGs were identified among the isolates from Israel. Representative testers of the three local VCGs were paired with tester strains of the OARDC (Ohio) international system and, based on strong complementation, 28 isolates were assigned to VCG2A, 158 isolates to VCG2B, and 378 to VCG4B. Ninety-two percent of VCG2B isolates were recovered from the northern part of Israel, and 90% of VCG4B isolates were from the south. Some overlap was observed in the central region. Isolates of the minor VCG2A were scattered among the two major VCGs, ranging from 8% (north) to 3% (south) of the isolates tested. No correlation was observed between VCG and host-plant of origin. Morphological differences were evident between isolates from different VCGs. When grown on CDA, isolates of VCG2B formed dark colonies with little or no aerial

mycelium whereas most of VCG4B isolates grew as colonies with dense aerial mycelium, were light gray and became dark gray only with age. All microstructures of VCG2B isolates were essentially larger than those of VCG4B. The very abundant, irregularly shaped microsclerotia of VCG2B isolates consisted of large cells, whereas the microsclerotia of VCG4B consisted of small cells, and were more spherical and scattered. VCG2A isolates exhibited intermediate morphology between VCG2B and VCG4B. VCG2A and VCG4B isolates had temperature optima of 24-27°C, and VCG2A grew faster than VCG4B isolates at 18-27°C. VCG2B isolates cumulatively showed lower and broad optimal growth temperatures, ranging from 18 to 24°C. None of the tested *V. dahliae* isolates grew at 35°C.

In Ohio pathogenicity studies of isolates from potato seed tubers, foliar symptoms of inoculated potato plants were visible 3-4 wk after inoculation and, in most cases, became more severe in plants inoculated with VCG 4A isolates than with VCG 4B (16, 20). Plants inoculated with VCG 4A isolates exhibited extensive chlorosis and some necrosis in the lower leaves, with symptoms occasionally extending to the upper leaves. In contrast, symptoms developed slowly on most plants inoculated with VCG 4B isolates and usually appeared as chlorotic areas generally restricted to the lower leaves. Necrotic areas rarely developed. Five to six weeks after inoculation, most plants inoculated with VCG 4A isolates were dead or nearly dead, whereas plants inoculated with VCG 4B isolates exhibited mild to moderate symptoms and only a few plants had died. After 8 wk, all plants inoculated with VCG 4A isolates were dead. Some plants inoculated with VCG 4B isolates were also dead, but most had symptoms that ranged from moderate to severe. A few showed senescence patterns only slightly more severe than the noninoculated control plants. Comparisons between mean AUSPC (area under senescence progress curve) values of all plants inoculated with VCG 4A and VCG 4B isolates that originated from the same state or province generally showed the same pattern of higher aggressiveness associated with VCG 4A isolates regardless of geographic location.

Field microplot tests of potato grown in soil infested with selected isolates of *V. dahliae*, both alone and in combination with root-lesion nematodes (*Pratylenchus penetrans*), were conducted in Ohio. In 1998, isolates recovered from potato seed tubers (three VCG 4A and five VCG 4B) were compared with Ohio reference strains of each VCG. With *V. dahliae* alone, the average AUSPC value for VCG 4A isolates was 27% higher than that for VCG 4B isolates. When inoculated in combination with *P. penetrans*, average AUSPC values were 44% higher for VCG 4A isolates.

Moreover, plants grown in the presence of VCG 4A isolates alone exhibited a higher average disease severity than those coinfecting with VCG 4B isolates plus *P. penetrans*. Total tuber weight was highly reduced in plants coinfecting with VCG 4A isolates plus *P. penetrans* compared with those treated with VCG 4B isolates plus *P. penetrans*. In 1999, similar tests were conducted using isolates obtained from Columbia Basin soils. As before, symptoms generally developed earlier and were more severe on plants infected with VCG 4A isolates, particularly when *P. penetrans* was also present. Unfortunately the 1999 growing season was quite hot and dry and differences in disease severity were less apparent as the season progressed regardless of isolate. However, synergistic interactions between *V. dahliae* and *P. penetrans* were more apparent with VCG 4A isolates.

Sixty one Israeli isolates were tested for pathogenicity to cotton and eggplant (12). Of these, 60 were pathogenic to both crops, and one was avirulent. Isolates that incited mild symptoms on cotton (AUDPC \_ 20%) were defined as non-defoliating (ND) pathotype. Other isolates caused severe foliar symptoms, stunting and often death but little or no defoliation of inoculated cotton plants (AUDPC \_ 26%), and were defined as defoliating-like (DL) pathotype. Differential aggressiveness of the isolates on eggplant was used to further define three subgroups among the ND pathotype and two subgroups within the DL pathotype. The subgroups were statistically supported by cluster analysis. Thus, isolates of the cotton-ND pathotype that caused mild symptoms on eggplant (AUDPC \_ 24%) were defined as pathotype ND1, those causing moderate-to-strong symptoms (AUDPC 26 to 50%) were defined as pathotype ND2, and those which caused severe symptoms (AUDPC \_ 55%) were defined as ND3. Similarly, within the cotton-DL pathotype, isolates that caused mild-to-moderate symptoms on eggplant (AUDPC \_ 26%) were defined as pathotype DL1 and those causing severe symptoms (AUDPC \_ 43%) were defined as pathotype DL2. Irrespective of their host or regional origin, all VCG2A and 86% of the VCG4B isolates (19 of 22) were of the ND2 pathotype, inducing mild wilting in cotton but moderate-to-strong levels of disease in eggplant. In VCG2B, all the isolates from cotton were of the DL1 pathotype, causing severe wilt in cotton and mild-to-moderate symptoms in eggplant. The remaining VCG2B isolates, of non-cotton origin, were highly variable.

Additional pathogenicity tests were conducted in Israel on potato and tomato using 86 Israeli isolates of VCGs 2A, 2B and 4B (25). In potato, disease symptoms appeared earlier in plants inoculated with VCG 4B isolates than in those inoculated with VCG 2A or VCG 2B isolates. In

addition, 30 days following inoculation AUDPC values were significantly higher for VCG 4B isolates as compared with VCG 2A and VCG 2B isolates. Colonization of potato stems was most extensive for VCG 4B isolates, intermediate for VCG 2A isolates and lowest for VCG 2B isolates. In tomato, disease symptoms appeared earlier in plants inoculated with VCG 2A isolates. AUDPC values were greatest for VCG 2A isolates, intermediate for VCG 4B isolates and lowest for VCG 2B isolates. Colonization of tomato stems was much more extensive with VCG 2A isolates than with the other two. Most isolates of *V. dahliae* in this collection that originated from potato and cotton are in VCG 4B and VCG 2B, respectively. To exclude the possibility that the observed differences between VCGs reflect mainly the origin hosts of the isolates, pathogenicity data from isolates originating from cotton, potato and eggplant were analyzed separately. The same differential patterns of pathogenicity and aggressiveness were observed in potato and tomato plants regardless of the host of origin, indicating that the observed differential aggressiveness of isolates is a characteristic of the isolate VCG.

## Discussion

Studies of vegetative compatibility in *V. dahliae* have shown that the fungus is comprised of three main VCGs, designated VCG1, VCG2, and VCG4 (11, 19). Each of these VCGs has been divided into two subgroups, based on quantitative differences in complementation reactions among *nit* mutants (9, 11). In Ohio studies, 65 of the 224 seed lots tested from across North America (nearly 30%) had tubers that were infected with *V. dahliae* (16, 20). Considering that only 20 tubers per seed lot were tested, it is likely that more seed lots were infected at lower rates that would not be detected by our methods. Based on these findings, it is clear that commercial seed lots grown across North America commonly contain many tubers infected by *V. dahliae* and that this is a primary method by which the pathogen is introduced into production fields. All isolates of *V. dahliae* from seed tubers were VCG 4. This finding correlates well with previous work on potato in the USA (9, 22, 23) and Europe (8) and with data reported here from Israel. In our study, *V. dahliae* isolates were obtained from a wide range of potato cultivars grown across North America. About two thirds of the isolates were VCG 4A, with the rest VCG 4B. There was no indication of significant differences in this pattern among groups of isolates obtained from different cultivars or geographic areas.

All *V. dahliae* isolates were pathogenic to potato although their aggressiveness varied widely. All plants inoculated with VCG 4A isolates were dead 7-8 wk after inoculation, whereas symptoms of plants inoculated with VCG 4B isolates varied widely. Although VCG 4A isolates were generally more aggressive than VCG 4B, some isolates in each VCG deviated from this pattern. Variation in aggressiveness among isolates in the same VCG is viewed by some workers as an indication of the presence of a continuum of aggressiveness rather than distinct pathotypes (1). However, data presented here strongly suggest that symptoms of potato early dying are more pronounced on plants infected with VCG 4A isolates, as compared with VCG 4B. This conclusion fits well with previous studies (5, 10, 23). Further evidence of this was found in field microplot studies in which VCG 4A and VCG 4B isolates also differed in their ability to interact with root-lesion nematodes, as we have reported previously (3). Results from our studies and others provide evidence for recognition of two distinct pathotypes among populations of *V. dahliae* recovered from potatoes in N. America. One pathotype, to which most VCG 4A isolates belong, leads to early and severe symptoms resulting in a rapid collapse and death of the plant. The other pathotype, composed of VCG 4B isolates, leads to slower development of symptoms which appear mainly as chlorotic areas on the leaves. A similar situation has been well documented in cotton where two pathotypes of *V. dahliae* occur, referred to as “defoliating” and “non-defoliating” strains, that differ in aggressiveness (6).

In Israel, three VCGs were identified among 565 isolates of *V. dahliae* isolated from several host plants (12). VCG2A and VCG 2B appear to be distinct entities, distinguished by their growth rate, morphology, pathogenicity, and regional distribution. VCG 2B and 4B form two main regional populations, VCG2B in the north and VCG4B in the south, with some overlap in the center. Isolates of VCG2A were scattered throughout all regions. On cotton, two pathotypes were evident: the ND pathotype caused weak-to-moderate symptoms, whereas the DL pathotype caused severe symptoms with little or no defoliation. All VCG2A, most of VCG4B and a few non-cotton VCG2B isolates tested belonged to the cotton-ND pathotype. All VCG 2B isolates from cotton were of the cotton-DL pathotype. Israeli tests with potato and tomato showed that VCG 4B isolates were most aggressive on the former and VCG 2A on the latter. Differential susceptibility of plant species to different pathotypes (VCGs) should be considered in resistance breeding, crop rotation and other strategies of disease management. VCG4A is common in *Verticillium*-wilt affected potato fields in North America, but was not found in Israel. *Verticillium dahliae* is known to have

been introduced into the Negev region of southern Israel with infected potato seed tubers from Europe, where it became established in many fields with expanding potato cultivation (15). The presence in Israel of only VCG4B is significant and bears watching.

### **Scientific implications.**

*Verticillium dahliae* was found to be commonly associated with seed potatoes produced in all parts of N. America. Genetic diversity among isolates was low in that the population was exclusively VCG 4. However, two distinct pathotypes were found, composed of VCG 4A and VCG 4B, the former being highly aggressive and most capable of interaction with root-lesion nematodes. Populations of *V. dahliae* isolated from several crops in Israel were genetically and phenotypically characterized: a VCG4B population which is less aggressive to cotton, but more so to potato, was dominant in the southern part of the country, while VCG2B which is highly aggressive to cotton was dominant in the north. VCG 2A was less common, but highly aggressive on tomato. This study demonstrates that different VCGs have distinct pathogenicity and aggressiveness on various crops and variable macroscopic and microscopic morphology and temperature-dependent growth rates. Strains belonging to the same VCG share common traits and may reflect a common history. The study of VCGs in *Verticillium* is important to improve our understanding of the pathogenic capabilities of various populations of this pathogen. This knowledge can shed light on the historical movements of the fungus and lead to improved management tactics. Our study on VCG population structure of *V. tricorpus* and *V. nigrescens* (14) is the first one on weakly pathogenic or saprophytic species of *Verticillium*.

**Potential impact on agriculture, industry, environment, policy, legislation.**

Our findings have broad implications for the North American potato industry. Extensive infection of seed potatoes with *V. dahliae* certainly explains the widespread distribution of VCG 4A strains across U.S. and Canadian potato production regions. It also brings into question the importance of seedborne as compared with soilborne inoculum of *V. dahliae*, the latter being the target of most current control practices. Considerable resources are expended annually in some production regions to fumigate fields prior to planting potatoes for control of potato early dying. The importance of seedborne inoculum in the development of potato early dying following fumigation warrants investigation. The use of disease-resistant cultivars is the most practical disease management strategy (8, 17, 18) and efforts are ongoing to develop cultivars with improved resistance to potato early dying and high market acceptance. Better understanding of the genetic diversity that exists among populations of *V. dahliae* that cause potato early dying and the use by breeders of the most aggressive strains, ie. VCG 4A, in screening germplasm will be essential to accomplish this goal. The information on genetic variability and pathogenic capacity of *V. dahliae* populations in Israel is of great importance to breeders aiming at developing disease-resistant cultivars and to those developing improved disease management programs for Verticillium wilt in major crops. Of special importance is the fact that a highly virulent pathotype of the pathogen is prevalent in cotton fields in the north. This information was brought to the attention of extension specialists, growers and the authorities in the Ministry of Agriculture in Israel. Special regulations were imposed to avoid spread of infested materials. As a result, special effort is now in progress by the Cotton Board to prevent spread of infected material during cotton transport and processing. Consideration should also be given to importation of seed potatoes from N. America with regard to avoiding introduction of VCG 4A which does not appear to be found presently in Israel. Since this disease is often controlled by soil fumigants, some of which will be phased out in the future, any contribution to disease management has both economic and environmental implications.

## References

1. Ashworth, L. J. 1983. Aggressiveness of random and selected isolates of *Verticillium dahliae* from cotton and the quantitative relationship of internal inoculum to defoliation. *Phytopathology* 73:1292-295.
2. Bao, J.R., Katan, J., Shabi, E., and Katan, T. 1998. Vegetative compatibility groups in *Verticillium dahliae* from Israel.. *Eur. J. Plant Pathol.* 104:263-269.
3. Botseas, D.D. and Rowe, R.C. 1994. Development of potato early dying in response to infection by two pathotypes of *Verticillium dahliae* and co-infection by *Pratylenchus penetrans*. *Phytopathology* 84:275-282.
4. Correll, J. C., Klittich, C.J.R., and Leslie, J.F. 1987. Nitrate nonutilizing mutants of *Fusarium oxysporum* and their use in vegetative compatibility tests. *Phytopathology* 77:1640-1646.
5. Corsini, D. L., Davis, J. R., and Pavek, J. J. 1985. Stability of resistance of potato to strains of *Verticillium dahliae* from different vegetative compatibility groups. *Plant Dis.* 69:980-982.
6. Daayf, F., Nicole, M., and Geiger, J. 1995. Differentiation of *Verticillium dahliae* populations on the basis of vegetative compatibility and pathogenicity on cotton. *Eur. J. Plant Pathol.* 101:69-79.
7. Dobinson, K.F., Harrington, M.A., Omer, M. and Rowe, R.C. 2000. Molecular differentiation of *Verticillium dahliae* vegetative compatibility group 4A and 4B isolates associated with potato early dying. *Plant Dis.* 84: (in press). Appendix XX

8. Jeger, M. J.; Hide, G. A.; Van Den Boogert, P.H.; Termorshuizen, A. J.; and Van Baarlen, P. 1996. Pathology and control of soil-borne fungal pathogens of potato. *Pot. Res.* 39:437-469.
9. Joaquim, R.R. and Rowe, R. C. 1990. Reassessment of vegetative compatibility relationships among strains of *Verticillium dahliae* using nitrate-nonutilizing mutants. *Phytopathology* 80:1160-1166.
10. Joaquim, T.R. and Rowe, R.C. 1991. Vegetative compatibility and virulence of strains of *Verticillium dahliae* from soil and potato plants. *Phytopathology* 81:552-558.
11. Katan, T. 2000. Vegetative compatibility in populations of *Verticillium* - An overview. Pages 69-86 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). *Advances in Verticillium research and disease management*. APS Press. St. Paul, MN, USA.
12. Korolev, N., Katan, J. and Katan, T. 2000. Vegetative compatibility groups of *Verticillium dahliae* in Israel: Their distribution and association with pathogenicity. *Phytopathology* 90: (in press). Appendix C.
13. Korolev, N., and Katan, T. 1997. An improved medium for selecting nitrate-nonutilizing (*nit*) mutants of *Verticillium dahliae*. *Phytopathology* 87:1067-1070.
14. Korolev, N., and Katan, T. 1999. Vegetative compatibility grouping in *Verticillium nigrescens* and *V. tricorpus*. *Mycol. Res.* 103:-65-76. Appendix B
15. Krikun, J., and Orion, D. 1979. *Verticillium* wilt of potato: Importance and control. *Phytoparasitica* 7:107-116.
16. Omer, M.A., Johnson, D. A., and Rowe, R.C. 2000. Recovery of *Verticillium dahliae* from North American certified seed potatoes and characterization of strains by

vegetative compatibility and aggressiveness. Am. J. Pot. Res. 77: (in press). Appendix XX.

17. Powelson, M.L., and Rowe, R.C. 1993. Biology and management of early dying of potatoes. Pages 111-126 in: Cook, R.J., Zentmyer, G.A., and Shaner, G. (eds). Annu. Rev. Phytopathol. Vol. 31.
18. Powelson, M.L., and Rowe, R.C. 1994. Potato early dying: Causes and management tactics in the eastern and western United States. Pages 178-190 in: Zehnder, G.W., Powelson, M.L., Jansson, R.K., and Raman, K.V. (eds). Advances in potato pest biology and management. APS Press. St. Paul, MN, USA.
19. Rowe, R.C. 1995. Recent progress in understanding relationships between *Verticillium* species and subspecific groups. Phytoparasitica 23:31-38.
20. Rowe, R.C., Johnson, D.A. and Omer, M.A. 2000. Vegetative compatibility analysis of strains of *Verticillium dahliae* from potato seed tubers and plants from western and eastern North America. Pages 95-99 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). Advances in Verticillium research and disease management. APS Press. St. Paul, MN, USA.
21. Schnathorst, W.C. 1981. Life cycle and epidemiology of *Verticillium*. Pages 113-114 in: Mace., M.E., Bell, A.A. and Beckman, C.H. (eds). Fungal wilt diseases of plants. Academic Press, New York.
22. Strausbaugh, C.A., Schroth, M.N., Weinhold, A.R. and Hancock. J.G. 1992. Assessment of vegetative compatibility of *Verticillium dahliae* tester strains and isolates from California potatoes. Phytopathology 82:61-68.
23. Strausbaugh, C. A. 1993. Assessment of vegetative compatibility and virulence of *Verticillium dahliae* isolates from Idaho potatoes and tester strains. Phytopathology 83:1253-1258.

24. Tsrer, L., Erlich, O., Amitai, S. and Hazanovsky, M. 1998. Verticillium wilt of paprika caused by a highly virulent isolate of *Verticillium dahliae*. Plant Dis. 82:437-439.
25. Tsrer, L., Hazanovsky, M., Mordechi-Lebiush, S. and Sivan, S. 2000. Differential virulence of *Verticillium dahliae* isolates from various vegetative compatibility groups to potato and tomato. Plant Pathology 49: (submitted). Appendix XX.

### List of publications for the project

#### Journal Articles

Bao, J.R., Katan, J., Shabi, E., and Katan, T. 1998. Vegetative compatibility groups in *Verticillium dahliae* from Israel.. Eur. J. Plant Pathol. 104:263-269.

Dobinson, K.F., Harrington, M.A., Omer, M. and Rowe, R.C. 2000. Molecular differentiation of *Verticillium dahliae* vegetative compatibility group 4A and 4B isolates associated with potato early dying. Plant Dis. 84: (accepted). Appendix A

Korolev, N., Katan, J. and Katan, T. 2000. Vegetative compatibility groups of *Verticillium dahliae* in Israel: Their distribution and association with pathogenicity. Phytopathology 90: 529-536.

Korolev, N., and Katan, T. 1997. An improved medium for selecting nitrate- nonutilizing (*nit*) mutants of *Verticillium dahliae*. Phytopathology 87:1067-1070.

Korolev, N., and Katan, T. 1999. Vegetative compatibility grouping in *Verticillium nigrescens* and *V. tricorpus*. Mycol. Res. 103:-65-76.

Omer, M.A., Johnson, D. A., and Rowe, R.C. 2000. Recovery of *Verticillium dahliae* from North American certified seed potatoes and characterization of strains by vegetative compatibility and aggressiveness. Am. J. Pot. Res. 77: (in press). Appendix B.

Tsrur, L., Erlich, O., Amitai, S. and Hazanovsky, M. 1998. Verticillium wilt of paprika caused by a highly virulent isolate of *Verticillium dahliae*. Plant Dis. 82:437-439.

Tsrur, L., Hazanovsky, M., Mordechi-Lebiush, S. and Sivan, S. 2000. Differential virulence of *Verticillium dahliae* isolates from various vegetative compatibility groups to potato and tomato. Plant Pathology 49: (submitted). Appendix C.

### **Invited book chapter**

Katan, T. 2000. Vegetative compatibility in populations of *Verticillium* - An overview. Pages 69-86 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). Advances in Verticillium research and disease management. APS Press. St. Paul, MN, USA.

### **Abstracts**

Korolev, N., Katan, J., and Katan, T. 1997. Diversity, distribution and properties of *Verticillium dahliae* vegetative compatibility groups (VCG) in Israel. Phytoparasitica 25:265.

Korolev, N. 1998. Virulence and VCG diversity in *Verticillium* spp. from plant tissue and soil. Phytoparasitica 26:241-242.

Korolev, N., Katan, J., Katan, T. and Gindin, G. 1998. Comparative study of genetic diversity in four *Verticillium* species in terms of vegetative compatibility. *Sixth International Mycological Congress*, Jerusalem, Israel., pg. 151.

Korolev, N., Katan, J., and Katan, T. 1999. Population structure of *Verticillium dahliae* in Israel. *XIVth International Plant Protection Congress*, Jerusalem, Israel, pg. 37.

Korolev, N., Katan, J., and Katan, T. 1999. New *Verticillium dahliae* pathotype highly aggressive to cotton in Israel. Phytoparasitica 27:144.

Korolev, N., Katan, J., and Katan, T. 2000. Genetic variation and virulence of *Verticillium dahliae* from different hosts in Israel. *Phytoparasitica* 28: (in press).

Omer, M., Beery, W., Johnson, D., and Rowe, R. 1997. Vegetative compatibility among isolates of *Verticillium dahliae* from potato seed tubers and stems from the western USA. *Phytopathology* 87: S72.

Omer, M. and Rowe, R. 1998. Virulence of two *Verticillium dahliae* pathotypes isolated from potato seed tubers. *Phytopathology* 88:S69.

Omer, M., and Rowe, R. 1999. Synergistic interactions of two *Verticillium dahliae* pathotypes and *Pratylenchus penetrans* on potato. *Phytopathology* 89:S57

Omer, M., Moiseenko, J. and Rowe, R. 2000. Recovery and distribution of *Verticillium dahliae* from potato fields in the Pacific Northwest. *Phytopathology* 90: (in press).

Rowe, R., Omer, M. and Johnson, D. 1998. North American potato seed lots -- A primary source of *Verticillium*? *Am. J. Potato Res.* 75:295.

Tsror (Lahkim) L., Hazanovsky M., Leviush-Mordechai, S. and Sivan S. 1999. Pathogenicity of *Verticillium dahliae* of different vegetative compatibility groups. *Phytoparasitica*, 27:144-145.

Tsror (Lahkim) L., Hazanovsky M., Leviush-Mordechai, S. and Sivan S. 1999. Pathogenicity of vegetative compatibility groups of *Verticillium dahliae* in Solanaceae. *Phytopathology*, 89:S78.

## **Proceedings**

Korolev, N., Katan, J., and Katan, T. 2000. Vegetative compatibility groups of *Verticillium dahliae*, their pathogenicity and regional distribution in Israel. Pages 87-91 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). *Advances in Verticillium research and disease management*. APS Press. St. Paul, MN, USA.

Korolev, N., Katan, J., and Katan, T. 2000. Vegetative compatibility among populations of *Verticillium tricorpus* and *V. nigrescens* in Israel. Pages 103-105 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). Advances in Verticillium research and disease management. APS Press. St. Paul, MN, USA.

Rowe, R.C., Johnson, D.A. and Omer, M.A. 2000. Vegetative compatibility analysis of strains of *Verticillium dahliae* from potato seed tubers and plants from western and eastern North America. Pages 95-99 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). Advances in Verticillium research and disease management. APS Press. St. Paul, MN, USA.

Tsrur, L., Erlich, O., Amitai, S. and Hazanovsky, M. 2000. Verticillium wilt of paprika caused by a highly virulent isolate of *Verticillium dahliae*. Pages 322-326 in: Tjamos, E., Rowe, R., Heale, J. and Fravel, D. (eds). Advances in Verticillium research and disease management. APS Press. St. Paul, MN, USA.